A new species of the *Litoria peronii* Complex (Anura: Hylidae) from Eastern Australia

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MARTIN, A. A., WATSON, G. F., GARTSIDE, D. F., LITTLEJOHN, M. J., & LOFTUS-HILLS, J. J. A new species of the *Litoria peronii* complex (Anura: Hylidae) from eastern Australia. *Proc. Linn. Soc. N.S.W. 103* (1), (*1978*) *1979*: 23-35.

A new species of hylid frog, *Litoria tyleri,* is described from coastal eastern Australia. *L. tyleri* is a member of the *L. peronii* complex; it differs from the other Australian members of the complex (*L. peronii* and *L. rothi*) in adult morphology and mating-call structure. *L. tyleri* is sympatric with *L. peronii* and *in vitro* hybridization tests show the two species to be reciprocally genetically incompatible; they also differ biochemically.

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INTRODUCTION

The *Litoria peronii* group of species includes *L. peronii* in Australia, *L. amboinensis, L. darlingtoni* and *L. everetti* in New Guinea and associated islands, and *L. rothi* in both Australia and New Guinea (Tyler, 1968; Menzies, 1976). In addition, Straughan (1966) and Tyler (1968) noted that an undescribed member of this complex occurs near Brisbane, Queensland. We have collected this undescribed species along eastern coastal Australia from south-eastern Queensland to Jervis Bay, New South Wales. The purpose of the present paper is to describe the new taxon and compare it with *L. peronii* and *L. rothi.*

Because we have encountered *L. rothi* only infrequently in the field, comparative data for this species include only morphology of preserved adults and larvae, and mating-call structure. For the new species and *L. peronii*, however, we have considerable field and experimental data, encompassing adult morphology, mating-call structure, life history, larval morphology, reciprocal artificial hybridization tests, and electrophoresis of haemoglobins and plasma proteins.

METHODS

Adult Morphology

Comparative morphological study was restricted to sexually mature males, and measurements were taken (to 0.1 mm) with vernier calipers or with a stereoscopic microscope and eyepiece micrometer. We have followed the methods and terminology of Tyler (1968), except that head length was measured to the mid-point of the tympanum. Abbreviations used in the text are: E-N/IN = eye to naris distance/internarial span; HL/HW = head length/head width; TL/S-V = tibia length/snout to vent length.

Mating-Call Structure

Mating calls were recorded in the field using a variety of tape recorders and microphones (e.g. EMI L2B, Nagra IIIBH, Tandberg 11-2 tape recorders; Beyer M-69, Beyer M-88, Grampian DP-1 microphones). Where possible, the recorded specimens were collected and lodged in the Department of Zoology, University of Melbourne research collection. Wet-bulb air temperatures (which approximate those of small frogs calling from elevated positions) were taken at or near the calling sites.

Recordings were analysed on an audiospectrograph (Kay 6061-B Sona-Graph) with playback on a Tandberg 11-2 tape recorder. One call of each individual was analysed, generally the last clear call in the recording sequence. Note and spectral characteristics were obtained from a note at or near the middle of each call. Characteristics of the calls were measured on the audiospectrograms using calibrated scales.

Artificial Hybridization Tests and Life History

Artificial hybridization tests were carried out in the field using the technique of Rugh (1962). *In vitro* crosses were made between individuals of the new taxon and *L. peronii,* all collected from a sympatric breeding assemblage at Ryan's Swamp, Caves Beach Reserve, A.C.T. For each interspecific cross a simultaneous intraspecific (control) cross was made. Progeny of control crosses provided material for life history descriptions; and for *L. peronii* additional larval material from Sarsfield, Victoria, derived from an *in vivo* fertilization on 3rd December, 1965, was examined. Embryos and larvae were reared initially in the field under fluctuating temperature conditions and, on return to the laboratory, in Holtfreter's Solution at 20 ± 0.5°C. Larvae were fed on boiled lettuce. Larvae of *L. rothi* were collected at Kununurra, W.A. on 24th February, 1977. Methods of fixation, measurement and illustration of embryonic and larval material follow those of Martin and Littlejohn (1966).

Blood Proteins

Plasma proteins and haemoglobins from 12 individuals of *L. peronii* (6 from Caves Beach Reserve; 6 from Ourimbah, N.S.W.) and 9 of the new taxon (7 from Caves Beach Reserve; 2 from Ourimbah) were analysed. Animals were etherized and ventrally dissected to expose the cardiac cavity. A *truncus arteriosus* was cut, and blood collected in heparinized microhaematocrit tubes. The tubes were flame-sealed, centrifuged at low speed (approximately 25 g) for 10 minutes, then broken at the interface between plasma and cells.

Electrophoresis was carried out on horizontal 5% acrylamide gel slabs using the method described by Gartside (1972). All separations were performed at room temperature using a continuous tris (tris-hydroxymethyl aminomethane) borate buffer (0.3 M tris; pH 8.7) and 250 volts constant voltage, provided by a Vokam stabilized power supply. Five μl of plasma were analysed from each individual. Electrophoresis of plasma was continued until bromphenol blue dye, added to human plasma controls on each gel, had migrated 7 cm from the origin: this took about two hours.

Plasma proteins were stained in 1% amidoschwartz 10B (Chroma Gesellschaft) in 7% acetic acid. Haemoglobins, prepared by washing cells twice in 0.9% sodium chloride and haemolysing them in a mixture of equal parts of toluene and distilled water, were stained in o-dianisidine using the technique of Owen and Smith (1961). All blood samples were fresh when analysed.

Description

Litoria tyleri n. sp.

Types

Holotype, mature male No. R64754, Australian Museum, Sydney; male paratypes: Nos R64755-R64764; female paratypes: Nos R64765, R64766. Type locality: Ryan's Swamp, Caves Beach Reserve, A.C.T., 14 km S of Huskisson, Shire of Shoalhaven, N.S.W. (35° 09′ 45″ S, 150° 40′ 00″ E). Collected by D. F. Gartside, M. J. Littlejohn, J. J. Loftus-Hills, A. A. Martin, I. F. Spellerberg and G. F. Watson, 21st October, 1969. South Australian Museum Nos R12248, R12251, R12254, R13267A, R13267B, R13267C, R13338A, R13338B, R13338C, all mature males from the Ourimbah area, N.S.W., are also nominated as paratypes.

Diagnosis

The *Litoria peronii* group is distinguished from all other frogs in Australia by the combination of the following characteristics:

(i) well-developed webbing and discs on both fingers and toes;
(ii) second finger longer than first;
(iii) dorsum light grey to brown with minute green flecks in life; and
(iv) posterior surfaces of thighs patterned with yellow and black.

L. tyleri can be distinguished from *L. peronii* and *L. rothi* by means of the following characters. In both *L. peronii* and *L. rothi* there is a dark edging on the supratympanic ridge; this dark line is absent in *L. tyleri*. In *L. rothi* the axilla is black, and the posterior surface of the thigh is black with a few yellow spots. In *L. peronii* the axilla is yellow with large black spots, and the thigh is yellow with coarse

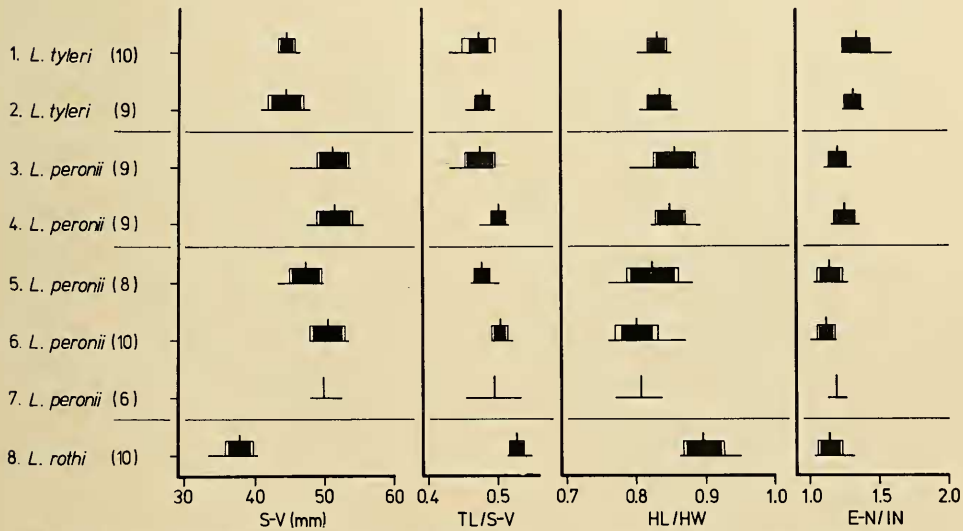

Fig. 1. Body dimensions and ratios of samples of *Litoria tyleri, L. peronii* and *L. rothi*. The number in parentheses after the species name is the sample size. The short vertical line is the sample mean and the horizontal line is the observed range of variation. The black bar represents the 95% confidence limits on either side of the mean and the open bar plus one-half of the black bar indicates one standard deviation of the mean. Sample localities are: 1 and 3, Caves Beach Reserve, A.C.T.; 2, Palm Grove, Ourimbah, N.S.W.; 4, Mallacoota, Vic.; 5, 5-19 km W of Coonabarabran, N.S.W.; 6, Narrandera, N.S.W.; 7, Yarrawonga area, Vic.; 8, Laura, Qld.

black variegation. In *L. tyleri* the axilla is yellow with few or no black spots, and the thigh is yellow with fine black variegation. The texture of the back is rough and warty in *L. peronii,* much less warty in *L. tyleri,* and virtually smooth in *L. rothi.* The mating calls of the three species are distinctive. *L. tyleri* has a greater S-V length than *L. rothi* (Fig. 1). Crosses between individuals of *L. tyleri* and *L. peronii* show the species to be reciprocally genetically incompatible (Table 1).

TABLE 1

Results of *in vitro* crosses between *Litoria tyleri* and *L. peronii* from Ryan's Swamp, Caves Beach Reserve, A.C.T.

Cross	No. of Eggs	No. Fertilized	% Hatched*
		L. tyleri ♀ × *L. peronii* ♂	
Control	110	96	100
Experimental	67	67	0
Control	100	100	80
Experimental	61	61	0
		L. peronii ♀ × *L. tyleri* ♂	
Control	40	40	70
Experimental	77	77	0
Control	65	65	60
Experimental	74	74	0

*Failure to hatch was associated with developmental breakdown, particularly abnormal neurulation.

The three species may readily be identified by the use of the following key:

1. A black line bordering the supratympanic ridge; axilla black, or yellow with heavy black spots; posterior surface of thigh heavily marked with black 2

   Supratympanic ridge without a black line; axilla yellow, sometimes with 1-2 small black spots; posterior surface of thigh yellow with fine black variegation ..... *L. tyleri*

2. Body length of mature males more than 42 mm; head length 76-88% of head width; back warty; posterior surface of thigh yellow with heavy black variegation ..... *L. peronii*

   Body length of mature males less than 42 mm; head length 86-95% of head width; back smooth; posterior surface of thigh black with a few yellow spots ..... *L. rothi*

Description

A medium-sized species of moderately slender habitus (Fig. 2). Vomerine teeth between the internal nares; tongue broad and with a posterior nick. Head broader than long (HL/HW = 0.80-0.85); snout rounded. External nares much closer to tip of snout than to eye; internarial span less than distance between eye and naris (E-N/IN = 1.23 −1.59). Canthus rostralis slightly concave but not sharply defined; loreal region sloping. Eye diameter slightly greater than distance from eye to naris,

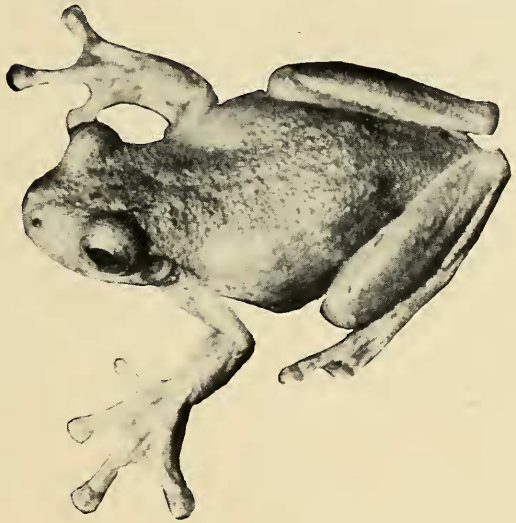

Fig. 2. Male paratype of *Litoria tyleri,* snout-vent length 44.0 mm.

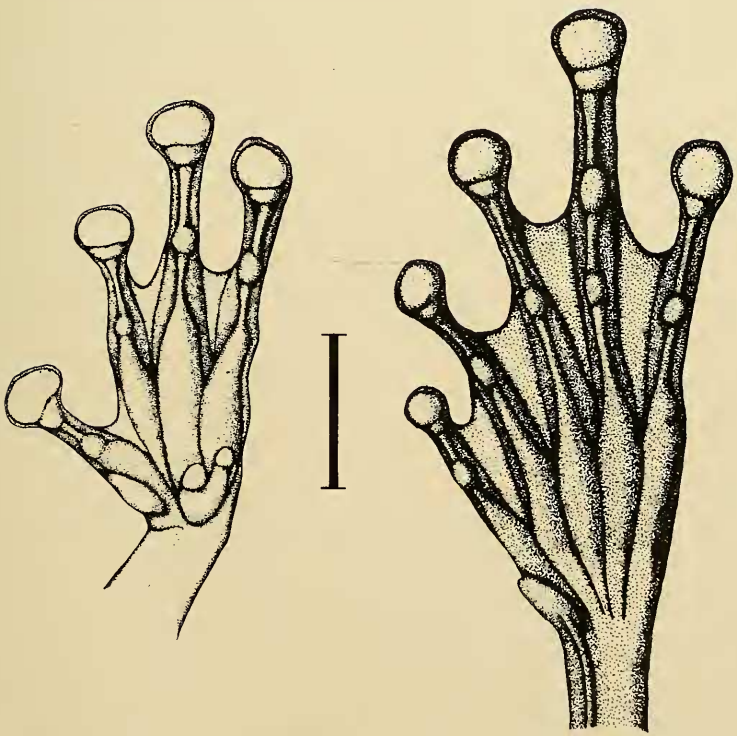

Fig. 3. Palmar view of left hand and plantar view of left foot of holotype of *Litoria tyleri.* The bar represents 5 mm.

and considerably greater than tympanum diameter. Tympanum prominent, bordered dorsally by a ridge running from behind the eye to the axilla.

Webbing on fingers well-developed (Fig. 3); discs prominent, disc diameter being about 1.5-2 times phalanx width. Sequence of lengths $3 > 4 > 2 > 1$.

Hind limbs moderately short; TL/S-V = 0.43-0.49. Webbing extends to penultimate phalanx of fourth toe and almost to discs of other toes (Fig. 3). Sequence of lengths $4 > 5 = 3 > 2 > 1$. Inner metatarsal tubercle small, oval; no outer metatarsal tubercle.

Dorsal skin mottled, light grey to medium brown, with minute emerald spots; texture finely warty. Ventral skin distinctly granular, off-white to yellowish. Gular region dusky brown in breeding males; no nuptial pads. Axilla with a yellow pterygial membrane, sometimes with 1-2 small black spots. Groin yellow with black mottling; posterior surface of thigh with finely divided yellow and black markings.

Dimensions of holotype are: snout-vent length, 43.4 mm; tibia length, 20.3 mm; head length, 12.8 mm; head width, 15.2 mm; eye to naris distance, 4.3 mm; internarial span, 3.1 mm; eye diameter, 4.7 mm; tympanum diameter, 3.3 mm.Dimensions and ratios of males in the type series are shown in Fig. 1. Dimensions of the two female paratypes are: snout-vent length, 47.6 and 45.6 mm; tibia length, 22.8 and 21.7 mm; head length, 14.3 and 14.1 mm; head width, 15.4 and 15.3 mm; eye to naris distance, 4.2 and 4.5 mm; internarial span, 3.7 and 3.7 mm; eye diameter, 4.9 and 4.4 mm; tympanum diameter, 3.8 and 3.5 mm.

Variation and Comparison with Other Species

The type series of *L. tyleri* shows little morphological variation, and a sample of males from Ourimbah, N.S.W., conforms with the type series (Fig. 1). Also shown in Fig. 1 are selected dimensions and ratios of two samples of *L. peronii* from coastal N.S.W. and Victoria, three samples of *L. peronii* from inland N.S.W. and Victoria, and a sample of *L. rothi* from Laura, Queensland.

L. rothi is the most distinctive member of the complex, having the smallest body size, longest legs and narrowest head. It also has the least warty dorsal skin and the greatest amount of black pigmentation in the axilla, groin and thighs.

Males of *L. tyleri* are intermediate between those of *L. rothi* and *L. peronii* in body size and degree of wartiness of the dorsal skin. On the other hand, *L. tyleri* has the shortest legs and the least amount of black colouration in the axilla, groin and thigh region.

Some differentiation between coastal and inland populations of *L. peronii* is evident, with the coastal samples tending to have a greater body size, narrower head and higher E-N/IN ratio.

Mating-Call Structure

The mating calls of the three species are of similar basic structure and consist of trains of regularly-repeated notes (Fig. 4), each of which is pulse modulated (Table 2).

Although there are insufficient data to assess the effects of temperature on call structure in the *L. peronii* group, general trends are evident for vocalizations in other species of anurans (Littlejohn, 1978). There is an inverse relationship with temperature for durations of calls and notes, and a direct relationship for repetition rates of calls, notes and pulses. The numbers of notes per call and pulses per note, and dominant frequency, usually are not markedly affected by temperature. Hence, allowance must be made for temperature variation when comparing calls.

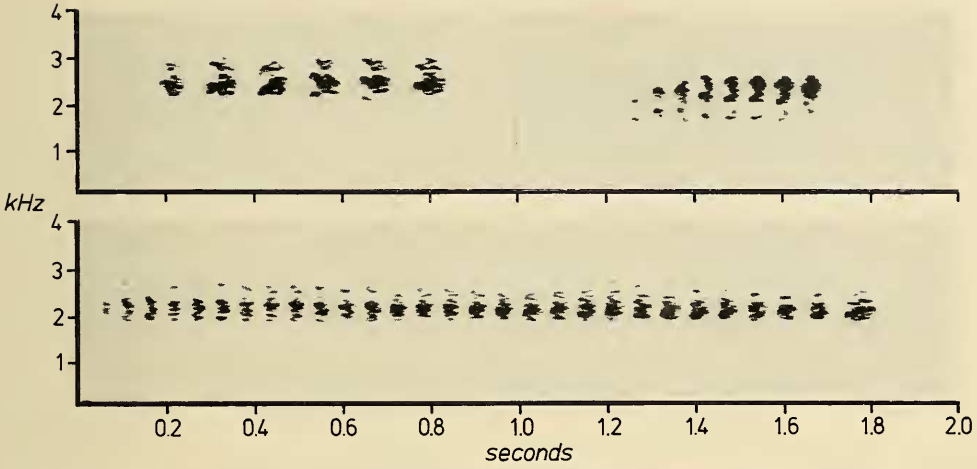

Fig. 4. Audiospectrograms of mating calls of: upper left, *Litoria tyleri,* Palm Grove, Ourimbah, N.S.W.; upper right, *L. rothi,* Kununurra, W.A.; lower, *L. peronii,* Palm Grove, Ourimbah, N.S.W. The trace for *L. peronii* is the latter half of a call.

Even so, it is clear that the calls of *L. peronii* are much longer than those of the other two species, and that the dominant frequencies are slightly higher and note repetition rates slightly lower in calls of *L. tyleri* (Table 2). There are more notes in the call of *L. peronii,* and more pulses in the notes of *L. tyleri* (Table 2). These latter meristic characters should be only minimally associated with temperature, and thus could be most useful in diagnosis.

Life History and Larval Morphology

The following descriptions are based on embryos and larvae reared from eggs of *L.. tyleri* and *L. peronii* fertilized *in vitro* at Caves Beach Reserve on 22nd October, 1969. The dimensions of seven newly-fertilized *L. tyleri* eggs (mean and range) are: embryo diameter, 1.32 mm (1.28-1.36); capsule diameter, 3.49 mm (3.20-3.60). The comparable figures for *L. peronii* are 1.52 mm (1.48-1.56) and 3.00 mm (2.80-3.12). Thus *L. tyleri* eggs are smaller, but with slightly larger capsules. In both species the animal pole is dark brown, the vegetal pole creamy-white, and the jelly capsule three-layered.

When 44 hours old, embryos of both species were at stage 18 of Gosner (1960). Those of *L. tyleri* are slender, medium brown in colour, and approximately 3 mm in total length. The *L. peronii* embryos are plumper, lighter in colour and shorter (length about 2.4 mm).

The embryos of *L. tyleri* hatched after 57 hours, at stage 20, when their total length was about 4.8 mm. Three pairs of external gills are present. Newly-hatched embryos of *L. peronii* are very similar but slightly lighter in colour; they hatched at an age of 70 hours.

All larvae were preserved at the age of 49 days, when they had reached stages 25-26. The dimensions (mean and range) of four *L. tyleri* larvae are: total length, 13.96 mm (12.80-14.72); tail length, 9.36 mm (8.80-9.76). Those of five *L. peronii* larvae are: total length, 19.50 mm (17.00-21.90); tail length, 12.20 mm (10.90-13.90). Apart from the difference in size, the larvae are generally similar, with those of *L. tyleri* having slightly heavier pigmentation and narrower tail fins. The mouth discs are not fully developed, but in the larvae of *L. tyleri* heavier pigmentation

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TABLE 2

Physical characteristics of mating calls of *Litoria tyleri, L. peronii* and *L. rothi*
Means and ranges are given

Species and Locality	Wet Bulb Air Temp. °C	Sample Size	Duration (msec)	Notes/Call	Note Repetition Rate (notes/sec)	Note Near Middle			
						Duration (msec)	Pulses/Note	Pulse Rep. Rate (pulses/sec)	Dominant Frequency (Hz)
Litoria tyleri									
Caves Beach Reserve, A.C.T.	12.0-13.0	4	1570 1270-2135	7.8 6-10	4.7 4.4-5.4	122 114-128	23.0 17-30	186 127-258	* 2250-2750
Palm Grove, Ourimbah, N.S.W.	20.8	4	614 455-830	6.0 5-8	9.3 8.6-10.3	64 60-68	23.8 23-25	374 347-392	2475 2350-2550
12.8 km NW of Coffs Harbour, N.S.W.	21.5	3	595 510-645	5.7 5-6	9.0 8.9-9.2	68 61-75	22.7 22-24	333 295-357	* 2150-2650
Litoria peronii									
Gipsy Point, Vic.	14.25-14.5	3	2647 2310-3270	34.7 29-44	12.9 12,4-13.3	43 38-51	10.7 9-12	239 220-276	* 1700-2000
Palm Grove, Ourimbah, N.S.W.	16.9-17.5	3	2425 2120-2800	42.0 36-50	17.3 16.9-17.9	30 25-33	9.3 9-10	308 267-356	* 1900-2100
Litoria rothi									
Kununurra, W.A.	25.6	3	443 370-490	8.3 7-9	17.8 17.4-18.2	25 25-26	10.0 9-11	378 356-400	1933 1850-2000

*Two equal peaks present in some calls.

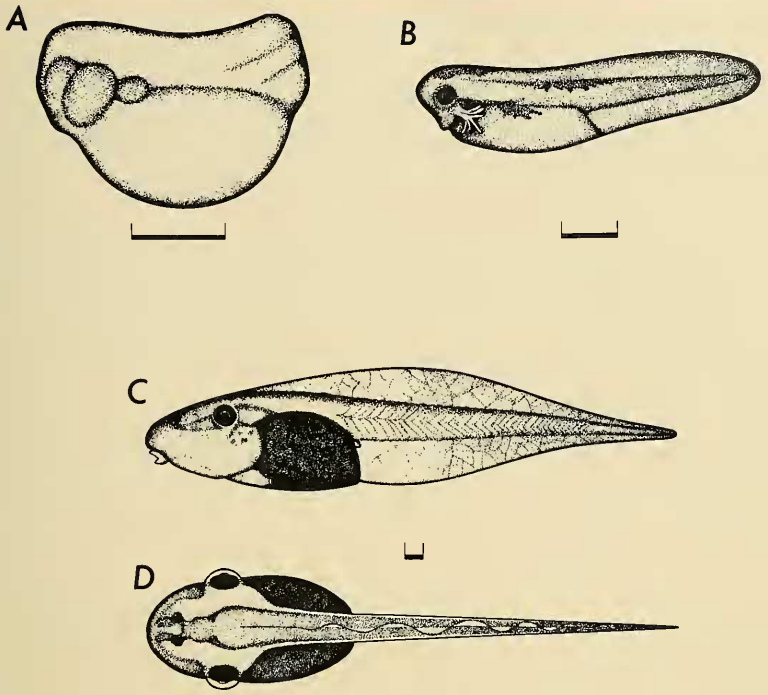

Fig. 5. Stages in development of *Litoria peronii*, Sarsfield, Vic. A, stage 17; B, stage 20 (newly-hatched); C and D, stage 29. The bar in each case represents 1 mm.

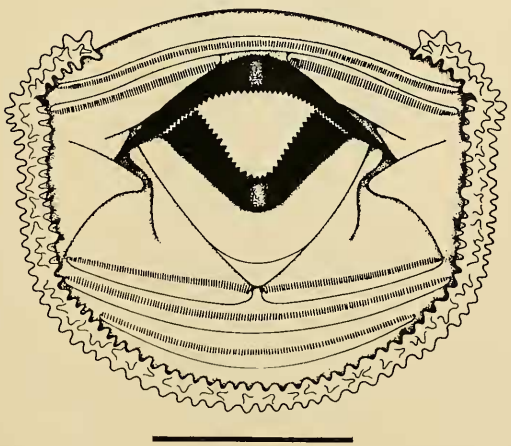

Fig. 6. Mouth disc of larva at stage 29 of *Litoria peronii,* Sarsfield, Vic. The bar represents 1 mm.

of the labial papillae is evident. In both species the spiracle is sinistral and the anus dextral.

Because a complete developmental series of *L. tyleri* from eggs to advanced larvae was not obtained, a series of *L. peronii* stages from Sarsfield, Vic., has been used for illustration (Fig. 5). Available material of *L. tyleri* indicates that the embryonic and larval stages of the two species are similar, and Fig. 5 shows the general characteristics of both species.

Live *L. peronii* larvae are pale golden-yellow, with a dark lateral stripe extending from the snout through the eye and along the dorsal edge of the body and tail musculature. The intestinal peritoneum is dark dorsally but silvery-white ventrally, and the oral and branchial areas are almost transparent but for scattered golden chromatophores. The most advanced larva in the series (stage 41) has a total length of 44.2 mm and tail length of 26.8 mm.

The mouth disc (Fig. 6) is typical of most Australian hylid larvae (Martin and Watson, 1971). There are two rows of teeth in the upper labium and three in the lower; 2-3 rows of papillae extend around the sides and back of the mouth disc. The mouth formula is

$$\frac{1 \quad 1 \quad 1}{1 \quad 2 \quad 1}$$

The Sarsfield larvae took about 190 days to develop from fertilization to metamorphosis, but the larval life-span of *L. tyleri* is unknown.

Fig. 7. Two-banded haemoglobin phenotypes of A, *Litoria peronii* and B, *L. tyleri,* both from Palm Grove, Ourimbah, N.S.W.

Fourteen *L. rothi* larvae from Kununurra, W.A., range in total length from 26.5 mm (stage 25) to 67.7 mm (stage 41). In general morphology they closely resemble the larvae of *L. peronii* and *L. tyleri*; however, their oral structure is distinctive. The lower jaw is much more robust than in the other species, and the third lower row of labial teeth is absent, or reduced to a small median structure bearing less than ten teeth.

Artificial Hybridization

Two *in vitro* crosses were made in both reciprocal combinations between *L. tyleri* and *L. peronii* (Table 1). While the control crosses displayed some degree of abnormality, the experimental crosses in both combinations were characterized by

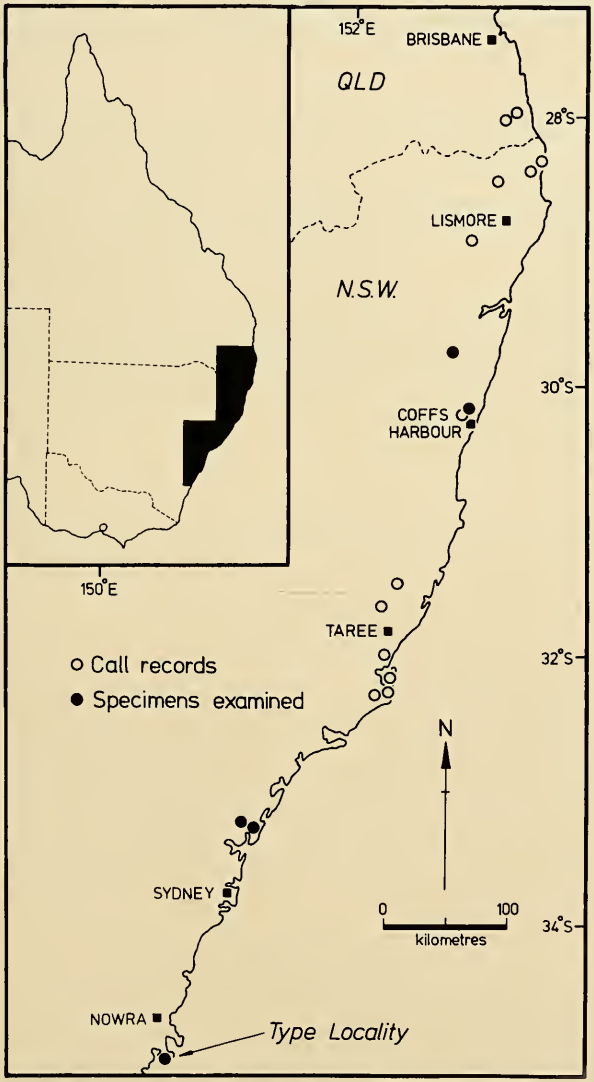

Fig. 8. The geographic distribution of *Litoria tyleri*. The inset shows the area of eastern Australia covered by the main map.

total developmental breakdown. No hybrid embryo successfully completed neurulation. This high degree of incompatibility is suggestive of crosses between diploids and tetraploids (as in the American *Hyla versicolor* and *H. chrysoscelis*; Wasserman, 1970), and a study of karyotypes would be of interest.

Blood Proteins

Fig. 7 shows the typical electrophoretic pattern for haemoglobins, each species having two anodally-migrating bands. The mobility of the leading band is similar in both taxa, while the mobility of the second band is consistently different. Migration of the second band is much faster in *L. tyleri* than in *L. peronii*. For plasma proteins, one set of bands appeared to be species-specific, although other bands in the complex plasma pattern differed in mobility or staining intensity between individuals. Despite this individual variability, bands which are presumed to be transferrins (based on experience with other hylids) are of similar mobility in every individual of both taxa.

Breeding Biology

Males of *L. tyleri* have been heard calling in October, November and January. Males called from the banks of permanent ponds and swamps, or from elevated positions (0.5-1.0 m above the water) in emergent or marginal vegetation. Wet bulb air temperatures at calling sites ranged from 11.0-21.5°C.

Reproductively active females have been collected in October.

Distribution

L. tyleri is distributed along the east coast of Australia from southern Queensland to the Jervis Bay area, N.S.W. (Fig. 8). The geographic range of *L. tyleri* is entirely included within that of *L. peronii* (see Moore, 1961, Fig. 50). Neither species is known to be sympatric with *L. rothi*, which is distributed along the northern and north-eastern coasts (Cogger, 1975).

Etymology

The species is named for Michael J. Tyler of the University of Adelaide, in recognition of his contributions to our knowledge of Australo-Papuan hylid frogs.

Conclusions

The three species of the *Litoria peronii* complex in Australia are readily distinguishable. The sympatric forms, *L. tyleri* and *L. peronii*, are highly distinctive in most aspects studied, including mating-call structure, blood-protein characteristics, and genetic incompatibility. The apparently absolute level of post-mating isolation between them renders the occurrence of hybridization extremely improbable. In any case, hybrids should be recognizable on grounds of adult morphology (e.g. Martin, 1972), mating-call structure (e.g. Zweifel, 1968) or blood-protein patterns (e.g. Brown and Guttman, 1970). None of our data for these characteristics is suggestive of the occurrence of hybridization.

Acknowledgements

The bulk of travel and running costs were met by an ARGC Grant (No. 66/16172) to M.J.L., and by the University of Melbourne research vote to the Department of Zoology. The Ian Potter Foundation provided funds for A.A.M. to visit Kununurra. We thank the South Australian Museum for the loan of specimens of *L. tyleri*. Dr I. F. Spellerberg assisted in the field, and Ms M. Leahy prepared some of the figures.

References

BROWN, L. E., and GUTTMAN, S. I., 1970.— Natural hybridization between the toads *Bufo arenarum* and *Bufo spinulosus* in Argentina. *Amer. Midl. Nat.*, 83: 160-166.

COGGER, H. G., 1975.— *Reptiles and amphibians of Australia*. Sydney: A. H. and A. W. Reed.

GARTSIDE, D. F., 1972.— The *Litoria ewingi* complex (Anura: Hylidae) in south-eastern Australia III. Blood protein variation across a narrow hybrid zone between *L. ewingi* and *L. paraewingi*. *Aust. J. Zool.*, 20: 435-443.

GOSNER, K. L., 1960.— A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16: 183-190.

LITTLEJOHN, M. J., 1978.— Long-range acoustic communication in anurans: An integrated and evolutionary approach. *In*: Taylor, D. H. and Guttman, S. I. (eds), *Reproductive Biology of Amphibians*. New York: Plenum.

MARTIN, A. A., 1972.— Studies in Australian Amphibia III. The *Limnodynastes dorsalis* complex (Anura: Leptodactylidae). *Aust. J. Zool.*, 20: 165-211.

——, and LITTLEJOHN, M. J., 1966.— The breeding biology and larval development of *Hyla jervisiensis* (Anura: Hylidae). *Proc. Linn, Soc. N.S.W.*, 91: 47-57.

——, and WATSON, G. F., 1971.— Life history as an aid to generic delimitation in the family Hylidae. *Copeia*, 1971: 78-89.

MENZIES, J. I., 1976.— *Handbook of common New Guinea frogs*. Wau: Wau Ecology Institute.

MOORE, J. A., 1961.— The frogs of eastern New South Wales. *Bull. Amer. Mus. Nat. Hist.*, 121: 149-386.

OWEN, J. A., and SMITH, H., 1961.— Detection of caeruloplasmin after zone electrophoresis. *Clinica chim. Acta.*, 6: 441-444.

RUGH, R., 1962.— *Experimental embryology*. Minneapolis: Burgess Publishing Company.

STRAUGHAN, I. R., 1966.— *An analysis of species recognition and species isolation in certain Queensland frogs*. Unpublished Ph.D. Thesis: University of Queensland.

TYLER, M. J., 1968.— Papuan hylid frogs of the genus *Hyla*. *Zool. Verhand.*, No. 96, pp. 1-203.

WASSERMAN, A. O., 1970.— Polyploidy in the common tree toad *Hyla versicolor* Le Conte. *Science*, 167: 385-386.

ZWEIFEL, R. G., 1968.— Effects of temperature, body size and hybridization on mating calls of toads, *Bufo a. americanus* and *Bufo woodhousei fowleri*. *Copeia*, 1968: 269-285.